

Site attachment and displacement of adults in two alpine metapopulations of *Somatochlora alpestris* (Odonata: Corduliidae)

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Abstract

Site attachment and displacement of adult *Somatochlora alpestris* were studied by means of mark-release-resighting during two years at two clusters of ponds (A, B) ca 8 km distant from each other on opposite slopes of Prättigau Valley in the Swiss Alps. Data on 127 marked teneralis in 1998 and 92 in 2000 at (A) were obtained. Additionally, in 1998, 187 and in 2000, 23 matures were marked at (A) and 162 at (B). No marked individuals were detected during the prereproductive period in the surroundings of the breeding sites. 14.0% of the males and 7.1% of the females marked as teneralis in 1998 were resighted at water subsequently. In 2000 the corresponding resighting rate was significantly lower due to a cold spell (4.0% and 2.4%, respectively). Only one male was resighted for the first time at its emergence pond. The resighting rates of marked adults at (A) were 59.2% (males) and 28.6% (females) in 1998, but only 5.6% and 0% in 2000, respectively. The corresponding resighting rates at (B) in 2000 amounted 27.1% (males) and 9.1% (females). Site attachment and displacement during the reproductive period differed between the two study sites. At (A) site attachment was modest and limited to the largest ponds. Many individuals shuttled between neighbouring ponds and some did so between waters distant up to 2 km from each other. Individuals at (B) exhibited stronger site attachment than at (A) with many being recorded exclusively at their marking water. No marked dragonfly was found to cross the main valley. We conclude that differences in site fidelity and displacement between the localities are due to weather conditions (affecting survival probability), population density (influencing competition) and separation of ponds by forest (inhibiting commuting flights).

Introduction

Anisopterans generally leave the water immediately after emergence, disperse during the maturation period and subsequently assemble at water for reproduction. For most species residing in temperate zones it is assumed that a fraction of the seasonal population returns to the emergence site while a number of individuals disperse and search for new habitats (for review see Corbet 1999). This account is based on only a few studies with individually marked adults in some libellulids (e.g. Pajunen 1962; Koenig & Albano 1987a; Soeffing 1990; Sternberg 1990; Michiels & Dhondt 1991) and aeshnids (Halverson 1984; Sternberg 1995a, 1995b; Inden-Lohmar 1997). Even less is known on homing, site fidelity and dispersal of corduliids. In *Somatochlora alpestris* (Selys) 25.0% of the males that were marked as teneral in the Black Forest (Germany) were recaptured by Sternberg (1990). In a Japanese population of *Cordulia aenea amurensis* Selys, Ubukata (1981) resighted between 36 and 50% of the male individuals that he marked as tenerals at the emergence water, but no exchange of adults between neighbouring breeding sites was observed. In an European population of *C. a. aenea* (Linnaeus) only 14% of the males were seen again at the emergence site (Ha 2000). On the other hand, she found some exchange of individuals within a group of breeding waters. The resighting rate of individuals that were marked as reproductively actives amounted 63% in *C. a. amurensis* (Ubukata 1981), 46% in *C. a. aenea* (Ha 2000) and 17% in *C. shurtleffii* Scudder (Hilton 1983).

The objective of this field study was to obtain information about return rates, site attachment and mobility in a "flier"-type species sensu Corbet (1962). We chose *S. alpestris*, a corduliid with mainly arcto-alpine distribution that, in Central Europe, occurs below and above the tree line. Two populations on mountain ridges in the eastern part of the Swiss Alps were selected. One was situated at an open, nearly treeless locality and the other on a terrain with highly fragmented spruce forest, both ca 8 km horizontally distant from each other, at different altitudes, and separated by a deep valley. The breeding waters of the study sites comprised two clusters of distinct small ponds, thus favouring the opportunity to test the metapopulation concept (Levins 1970).

Here we present the results of a two years' mark-release-resighting study that involved the following problems: (1) What are the resighting rates of individuals that were marked as tenerals or as matures? (2) Where do immatures spend their prereproductive period? (3) To what extent do reproductively active individuals exhibit site attachment and displacement within a cluster of neighbouring ponds? (4) Is there regular exchange of individuals between patchily distributed sub-populations? (5) Do both sexes visit suitable water bodies apart from the breeding centre? (6) Do they cross the main valley?

Study sites and methods

Study sites

This study was carried out in 1998 and 2000 during the emergence and reproductive period of *Somatochlora alpestris* from mid June to the end of August at a number of

breeding waters situated in the subalpine region of the Central Alps. Study sites were two localities in the Prättigau Valley, ca 22 km and 14 km NE of Chur (canton Grisons, Switzerland), about 8 km distant from each other: (A) Valpun region ($46^{\circ}57'N$, $09^{\circ}46'E$) and (B) Furner Berg ($46^{\circ}56'N$, $09^{\circ}39'E$) (Figs 1 and 2).

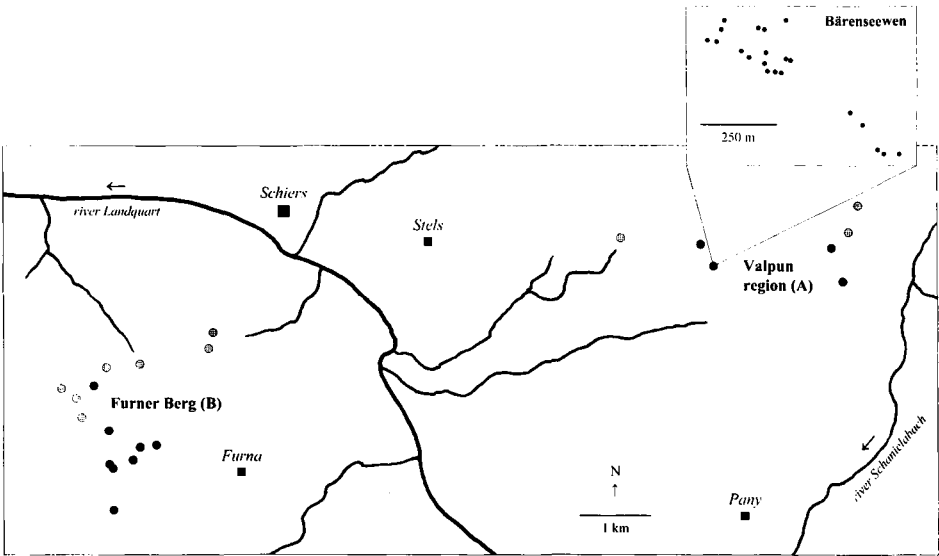


Figure 1. Overview of the ponds (black dots) at the study sites Valpun Region (A) and Furner Berg (B) in the Prättigau Valley (Grisons, Switzerland) with detail view of the Bärenseewen plateau; grey dots refer to other nearby breeding sites of *Somatochlora alpestris* with only small populations not included in this study. Villages (black squares) and rivers (lines).

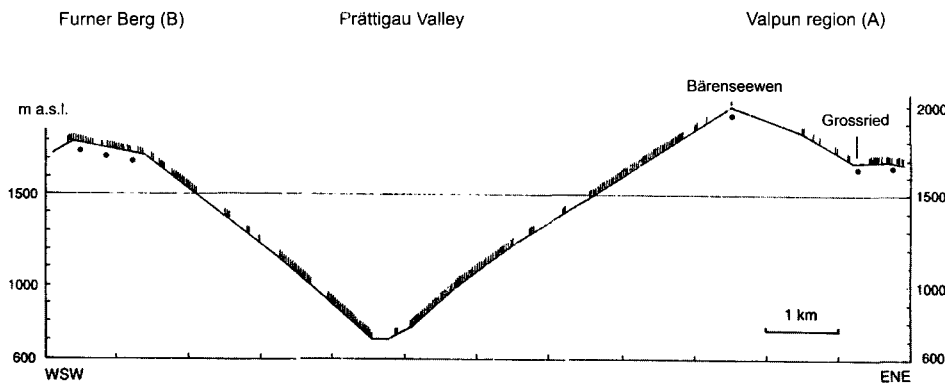


Figure 2. Cross section of the Prättigau Valley S of Schiers with study sites (A) and (B). Forested slopes are indicated by vertical bars, breeding sites of *Somatochlora alpestris* by dots.

Locality (A) was situated on the south-facing slope of the Prättigau Valley. The study concentrated on the Bärenseewen, a longitudinal plateau comprising approximately 10 ha and more than 20 small ponds at 1,970–2,040 m a.s.l., 100–150 m above the upper limit of the subalpine spruce forest (thermic level 2 sensu Schreiber 1977). It consisted mainly of treeless alpine pasture interspersed with *Rhododendron ferrugineum*-shrubs. Most ponds were partly overgrown with aquatic and marsh vegetation comprising *Sparganium angustifolium*, *Callitriche palustris*, *Eriophorum scheuchzeri*, *Carex nigra*, *C. canescens*, *C. echinata* and *Juncus filiformis* on peat ground. Six additional localities 250–2,000 m apart from the Bärenseewen ponds were regularly checked (Fig. 1), these mainly being situated within pastures at altitudes between 1,670 and 1,900 m, at thermic levels 2–4. Most ponds were small and lay in open terrain (Grün Wald, Grossried, Schaflucken), only Lengried/Capelgin and, to a lesser extent, Stelsersee and Riedbüel, were surrounded or bordered by forest.

Site (B) comprised a hilly area of about 2 km² on the north-facing side of the valley. It consisted of a mosaic of spruce forest fragments, hay meadows, pastures, small bogs and about 20 ponds between 1,710 and 1,820 m a.s.l. (thermic level 3). Eight of them (Fig. 1) were regularly checked. In contrast to the Bärenseewen plateau most ponds were scattered with distances more than 500 m between them. Some were situated in clearings of coniferous forest (Höhsäss central, Güferlitz E, Güferlitz central), while others (Chalberalp, bog Güfer and Anhornen) lay in a more open landscape with pastures and small bogs. For additional information on localities and the Odonata fauna, see Wildermuth (1986b) and Knaus (1999).

Methods

The conventional mark-release-resighting method was used. We applied quick drying nail varnish (bright yellow, red, blue, green) that was diluted 4:1 with acetone. Prior to marking, tenerals were taken from their emergence support as soon as their abdomen had reached the full length and kept in a gauze cage overnight. The following day, when the cuticle had hardened, the imagines were marked individually, thus minimising possible damage to the soft wings. Matures were netted for marking at the ponds while patrolling or ovipositing. Marks were applied on one or two positions of each wing (basal or distal half), providing up to 8 marking sites and allowing for identification of 255 individuals if all 8 locations were used with only one colour. In order to facilitate identification, different colours on fore and hind wings were applied. With this marking system we were able to identify the individuals even in rapid flight. Tenerals and matures recovered from this procedure in most cases without damage and behaved normally. Only in 1998 the maiden flight was unsuccessful for 8 marked tenerals (3 ♂, 5 ♀) because of the increased wing load; they were not included in the results. Resighted individuals were identified by eye or with close-focusing binoculars.

During the emergence period we concentrated on the Bärenseewen ponds at site (A) in both years. Here we marked 127 tenerals between 19 June and 5 July 1998 (in total 13 marking days) and 92 tenerals in the second study year between 17 June and 7 July 2000 (8 marking days; Table 1). The numbers are to compare with the total emerging popu-

lation that was determined by daily collection of exuviae: According to the number of exuviae the population comprised 674 and 254 individuals in 1998 and 2000, respectively (Knaus 2000; P. Knaus & H. Wildermuth unpubl.). In addition, at locality (A) 187 mature adults were marked from 6 July until 20 August 1998 (in total 18 marking days). In the second year, due to a spell of cold and wet weather from 8 until 16 July with the lower limit of snowfall sinking to 1,300–1,800 m on 11 July (see Wildermuth & Knaus 2002), only 23 adults were marked between 1 and 31 July 2000 (6 marking days). Therefore, during the reproductive period of the second study year, we focussed on locality (B). Here we marked 162 matures between 5 July and 15 August 2000 (8 marking days; Table 1).

Displacement of individuals was determined by connecting the initial release and the successive resighting sites with straight lines on the map, thus reflecting the shortest distance between two localities and not corresponding to the natural flight line that remained unknown.

For analyses of the displacement during the prereproductive period only data from individuals marked as tenerals and resighted within 35 days were considered (see Inden-Lohmar 1997). By making this restriction, the inclusion of possible movements during the reproductive period should be avoided to a large extent, since the mean duration of the maturation period was, according to marked individuals, 26.5 and 30 days for males and females, respectively (Knaus 1999). Nine of 13 individuals met this condition in 1998, two of three in 2000.

Duration and frequency of observation varied according to the weather conditions and to the number of collaborators available. On most days only one person collected data at locality (A) and/or (B). Due to the weather conditions that changed rapidly and unpredictably and to the lack of a sufficient number of field assistants the observation frequency could not be standardised. In 1998 we stayed 53 days in the study area, in 2000 only 21 days, mainly because of the cold spell mid July. We checked the ponds between 05:15 and 17:45 h solar time, chiefly between 07:00 and 16:30 h. The mean observation time at one pond was about one hour, but ponds with regular presence of *S. alpestris* were more intensively checked.

Statistical analyses

Parts of the data were analysed with logistic regressions (i.e. comparison of resighting rates between age and sex classes, rate of commuting flyers). Hereby the stepwise backward method was used with $p = 0.1$ for the exclusion of a variable from the model. Non-parametric tests like Fisher's exact Probability-Test and Mann-Whitney-U-Test were also employed. Further details to the statistical tests are given with the corresponding results. All tests were carried out two-tailed with SPSS, version 9.0 (SPSS, Inc.); the limit of significance was at $p = 0.05$.

Results

Resighting rates and visiting frequency

The resighting rates differed considerably between study year, locality, sex and age of marked individuals (Table 1). At locality (A), 10.2% individuals marked as tenerals were resighted in 1998 and only 3.3% in 2000. The difference between the two study years is even greater in the individuals that were marked as matures: In 1998 the resighting rate was 53.5% and two years later 4.3% only. At site (B) the resighting rate of marked matures in 2000 amounted 24.7%. Records of marked females were always distinctly rarer than those of marked males. Differences in resighting rates between age classes (tenerals/matures) and sexes for locality (A) in 1998 are highly significant (logistic regression: $n = 314$, $df = 2$, $\chi^2 = 80.092$, $p < 0.001$). Due to the low number of resightings for 2000, no statistical tests were performed. At site (B) in 2000 the resighting rate was significantly higher for males than for females (logistic regression: $n = 162$, $df = 1$, $\chi^2 = 3.977$, $p < 0.05$).

Table 1. Number of tenerals and adults of *Somatochlora alpestris* marked and resighted at study sites (A) and (B) in 1998 and 2000 and resulting resighting rates (in brackets). TM and TF: number of individuals marked as teneral males and females, respectively; AM and AF: number of individuals marked as adult males and females, respectively.

Study site	TM		TF		AM		AF	
	marked	resighted	marked	resighted	marked	resighted	marked	resighted
A - 1998	57	8 (14.0%)	70	5 (7.1%)	152	90 (59.2%)	35	10 (28.6%)
A - 2000	50	2 (4.0%)	42	1 (2.4%)	18	1 (5.6%)	5	0 (0%)
B - 2000	0	—	0	—	140	38 (27.1%)	22	2 (9.1%)

Males were resighted up to 15 times (mean = 3.8), females up to 3 times (mean = 1.5), the difference being significant (Mann-Whitney-U-Test: $n = 113$, $Z = -3.416$, $p < 0.001$). The time interval between two subsequent resightings at water in 1998 was 0–37 d (mean = 3.5 d) in marked adult males and 0–20 d (mean = 9.1 d) in adult females. In males 30.7% of the subsequent resightings were recorded at the same day and 66.5% within the first 4 subsequent days. Females visited the breeding sites significantly less frequently than males (Mann-Whitney-U-Test: $n = 100$, $Z = -2.4519$, $p < 0.05$).

Displacement during and homing after the prereproductive period

Despite of intense searching for immatures on five days between 27 June and 6 July 1998 in the wider surroundings of the Bärenseewen at site (A) no individuals could be detected. Only immature and mature individuals of *Aeshna juncea* (Linnaeus), *Cordulia*

aenea and *Leucorrhinia dubia* (Vander Linden), all reproducing in the region, were seen at a few sites within a range of 150–700 m away from the Bärenseewen.

In the same year six males and two females marked as teneral were resighted for the first time, i.e. immediately after the maturation period, at the Bärenseewen ponds, but only one of the males was first seen flying at his emergence water. Another male was first resighted at Schaflucken, 1,700 m apart from his emergence site. In 2000, two males marked as teneral were resighted for the first time at the Bärenseewen plateau, but not at the water of their origin.

Displacement and site attachment during reproductive period

Displacement and site attachment of adults at site (A) recorded in 1998 are summarized in Figures 3, 4 and 5. Although some marked dragonflies were seen again at their marking pond, the initial return rate was low: Only 13.0% of adults (12 ♂, 1 ♀) were resighted for the first time at the place where they were marked. Most movements occurred between ponds of the Bärenseewen plateau, i.e. between the ponds no. 3/9 and 3/21 as well as between the neighbouring ponds no. 8/9 and 19/20 (Fig. 3). At 23 water bodies at least one marked dragonfly was recorded during the flying season.

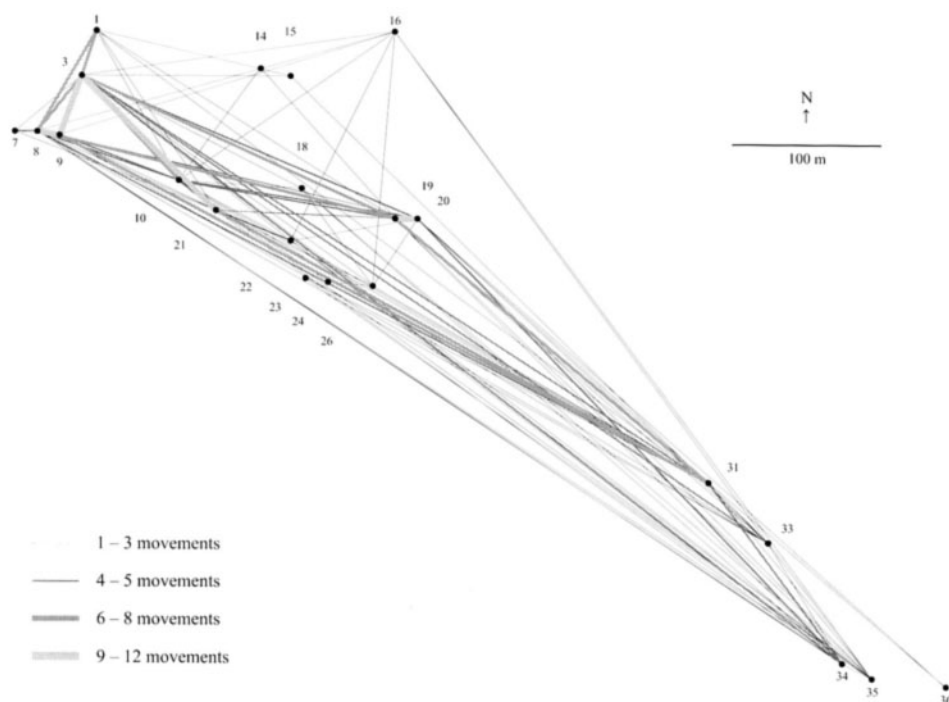


Figure 3. Mobility of *Somatochlora alpestris* at study site (A) within the Bärenseewen plateau between 20 June and 30 August 1998 ($n = 109$). Figures refer to pond numbers. All movements are shown except successive resightings at the same pond (cf. Fig. 4). The lines link two sites with successive records of the same individual.

The small ponds no. 31–36, slightly apart from the others, were also regularly visited. No correlation was found between the number of exuviae and the abundance of adults at corresponding waters. Site attachment was moderate and limited to the largest ponds (no. 3, 21 and 31; Fig. 4). In total 90 successive resightings were recorded at the same pond, amounting 46.0% of all resighted individuals (49 ♂, 3 ♀).

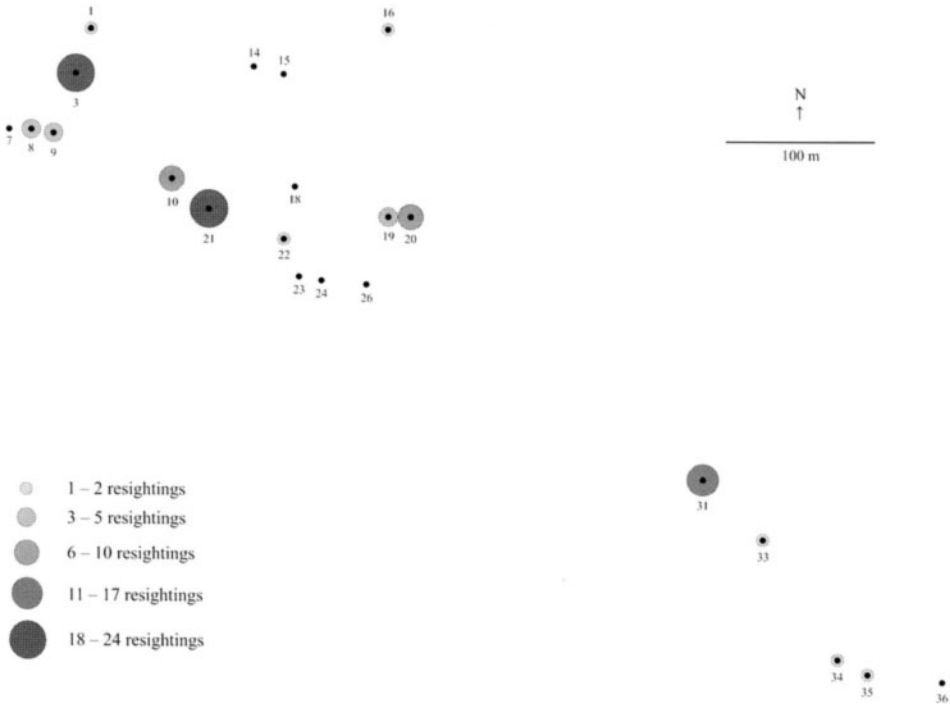


Figure 4. Site attachment of *Somatochlora alpestris* at study site (A) within the Bärenseewen plateau between 20 June and 30 August 1998 ($n = 52$). Figures refer to pond numbers. Grey circles refer to the number of successive resightings at the same pond. Only successive resightings at the same pond are presented (cf. Fig. 3).

18.6% of the resighted individuals (17 ♂, 4 ♀) were recorded at least once outside the marking area of the Bärenseewen plateau at site (A), accounting for 30 of the 397 (7.6%) resightings. These individuals were encountered at the ponds of Grün Wald, Grossried and Schaflucken. Despite repeated controls no marked dragonflies were found at three further water bodies in the Valpun region. Although the numbers are small, the nearly equal sex ratio of the individuals marked as teneral and resighted outside the Bärenseewen (i.e. ponds of Grün Wald, Grossried and Schaflucken) is noteworthy (Table 2). In contrast, males marked as adults were more often encountered away from the Bärenseewen than females of the same group. Commuting fliers were significantly more common among the individuals marked as teneral (53.8% of 13) than among those marked as adults (16.0% of 100; Fisher’s exact Probability-Test, $p < 0.0035$).

Table 2. Total number of resighted individuals of *Somatochlora alpestris* marked as tenerals and adults outside the Bärenseewen plateau at site (A) in 1998 and minimum distances to the Bärenseewen given in brackets. Abbreviations as in Table 1.

Locality	TM	TF	AM	AF
Grün Wald (250 m)	1	1	9	0
Grossried (1,520 m)	2	2	5	0
Schaflucken (1,560 m)	1	0	0	1

Movements between the Bärenseewen ponds and those in the surroundings, including the foraging areas, as well as the successive records of marked individuals at the same pond apart from the Bärenseewen are shown in Figure 5. Most resightings originated from the ponds of Grossried and Grün Wald. Some individuals shuttled between the localities. The maximal distances covered between two sites of resighting were 2.1 km and 1.9 km respectively for both sexes. Two males travelled in total at least 3.9 km and 7.5 km, one female at least 2.1 km. The resighting history of a male that was marked on 18 July at pond 19 of Bärenseewen is of particular interest: It was encountered again 3.5 h after marking at the same pond, then at pond 10 of Bärenseewen the following day, on 26 July at Grossried, on 7 August again at pond 19 of Bärenseewen, on 10 August back at Grossried and finally on 12 August at Grün Wald.

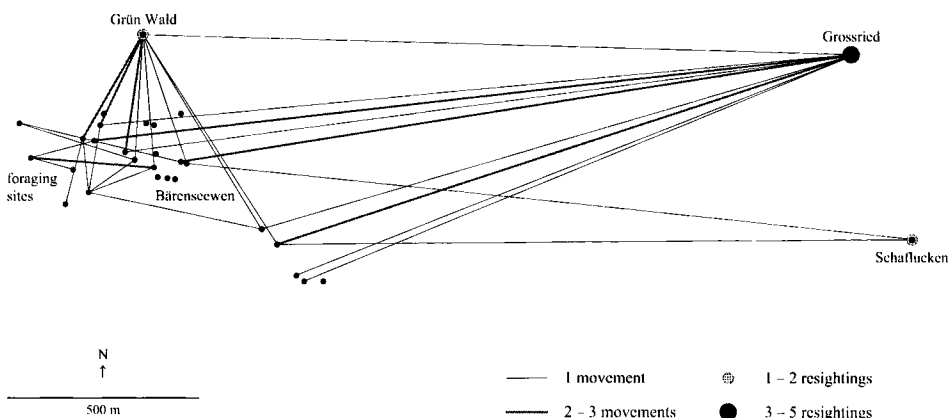


Figure 5. Mobility and site attachment of *Somatochlora alpestris* at study site (A) between the Bärenseewen and neighbouring sites from 19 June to 26 August 1998 ($n = 27$). All recorded movements between ponds or foraging sites (lines) and successive resightings at the same pond (circles) are shown.

For site (B) in 2000, the movements between the different ponds as well as the successive records of marked individuals at the same pond are given in Figure 6.

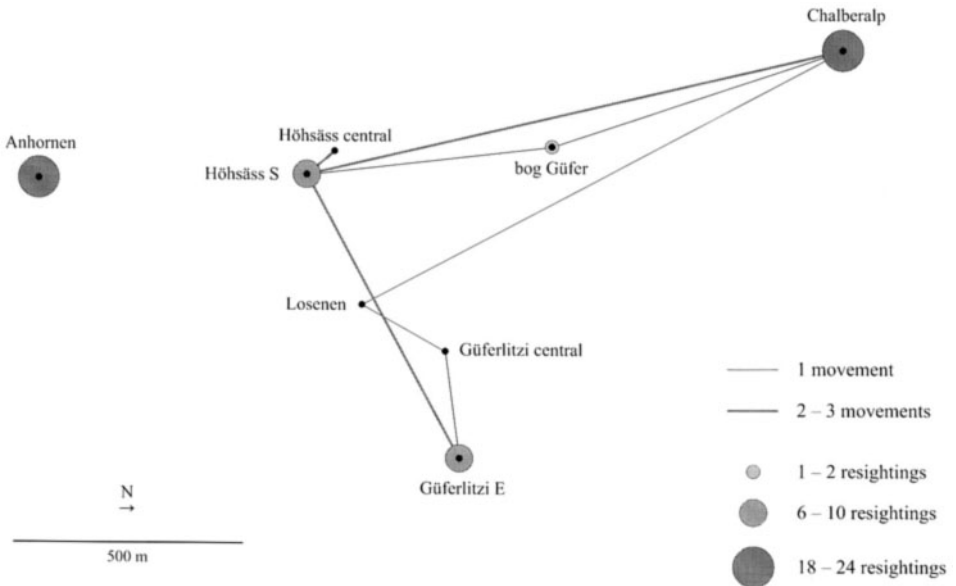


Figure 6. Mobility and site attachment of *Somatochlora alpestris* at study site (B) between 5 July and 25 August 2000 ($n = 40$). All recorded movements between ponds (lines) and successive resightings at the same pond (circles) are shown.

Most observations were made at the ponds Chalberalp, Anhornen and Höhsäss S. 25.0% of 40 marked adults (10 ♂) were resighted away from the ponds where they were marked. Most movements occurred between Höhsäss S and Höhsäss central, Güferlitz E and Chalberalp, respectively. Obviously little exchange took place between the localities and site attachment was more pronounced: 77.5% of all marked individuals (29 ♂, 2 ♀) were resighted for the first time at their marking pond. Moreover, 63 resightings of marked adults (82.9%) were made successively at the same pond, referring to 85.0% of the resighted individuals (32 ♂, 2 ♀). In particular, pond Anhornen was outstanding by its apparent isolation: all 10 males that were marked at this pond and resighted afterwards were recorded here again exclusively, but no other marked dragonfly from other waters arrived at this site. The maximal distance between two resighting localities for males was 1.2 km, this being also the maximum sum of the distances covered by one individual. The two resighted females were recorded again only at the marking site.

Differences in site attachment between both metapopulations are also evident in the mean value of all distances between two resighting localities covered by the same individual, i.e. the total of all distances between two resighting localities of one individual divided by its number of resightings (Fig. 7). These mean distances for resighted adults were significantly larger at site (A) than at (B) (Mann-Whitney-U-Test: $n = 140$, $Z = -4.960$, $p < 0.001$).

No dragonfly that was marked at locality (A) or (B) was resighted on the opposite side of the Prättigau Valley.

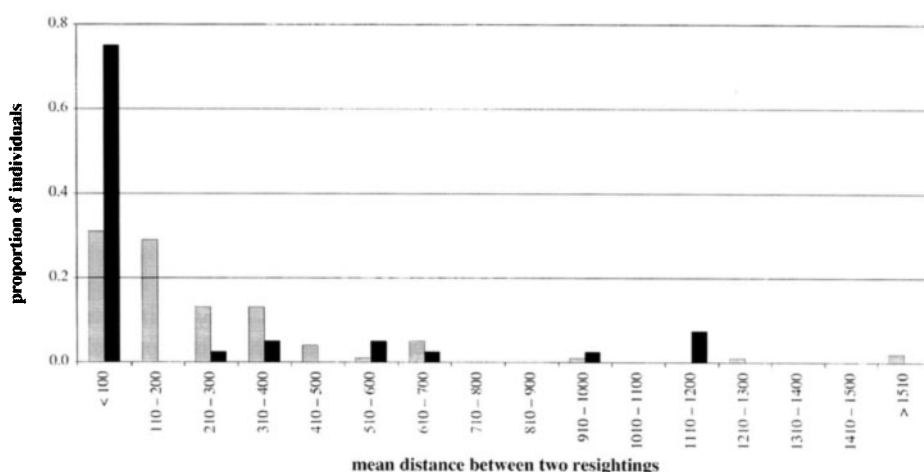


Figure 7. Mean value of all distances between two resighting localities covered by the same individual of *Somatochlora alpestris* at study site (A) in 1998 (grey, $n = 100$) and study site (B) in 2000 (black, $n = 40$).

Discussion

Resighting rate

Regular resightings of marked individuals clearly demonstrate that some males and females of *Somatochlora alpestris* remain in a distinct region and visit repeatedly the same localities. However, the resighting rates differed strikingly between study years, localities and sexes. Differences were also evident between individuals that were marked as teneral and those marked as matures. Several reasons may account for these findings, some of them probably being based on methodical or environmental factors that could not be standardised.

- (1) **Methods:** Marking procedure, observation frequency and characteristics of the ponds selected for recording might have affected the resighting rate. Although the insects were cautiously handled when capturing and marking, a possible “marking effect” can not be completely excluded, as pointed out by several authors (Koenig & Albano 1987b; Michiels & Dhondt 1991; Inden-Lohmar 1997; Flöss 1998). Keeping the teneral in a cage overnight prior to marking entails, in our view, only minimal impairment of the behaviour. Under natural conditions, rain, cold weather or emergence in the late afternoon can postpone the maiden flight until the following day. Furthermore, no difference was noted in the maiden flight between teneral that were released after marking and those that started spontaneously (Knaus 2000). The lower resighting rates of marked adults in 2000 compared to 1998 may partly be attributable to fewer days with observation activity in the second study year. Furthermore the time that was spent at water by the observers varied, and so did their attraction for dragonflies, the latter probably being related to the pond size.

- (2) Population size: In 1998 the size of the emerging population at Bärenseewen ponds was 2.6 times larger than in 2000 (Knaus 2000; P. Knaus & H. Wildermuth unpubl.). This might be responsible partly for the lower frequency of observation in 2000, as Inden-Lohmar (1997) presumed for similar findings in *Aeshna cyanea* (O.F. Müller). Sternberg (1999) reported on multiple year dynamics of population size of *S. alpestris* that was detected synchronously in two stem habitats more than 3 km apart: the abundance increased continuously during three or four years. When the local maximum emergence sum was reached the imagines dispersed almost completely in the following two years.
- (3) Survival probability: At site (A) the survival probability of the imagines was considerably lower in 2000 than in 1998. This was caused by an exceptionally long lasting cold spell with snowfall in mid July 2000 (Wildermuth & Knaus 2002). The fact that only three of 92 individuals marked as teneral were resighted demonstrates that very few imagines survived this period. This is in accordance with the view of Inden-Lohmar (1997) who assumes that the resighting rate is strongly affected by the weather conditions during the flying season. This was confirmed for *S. flavomaculata* (Vander Linden) (Flöss 1998). In addition, the resighting rate also depends on the age at which the imagines are marked. In individuals marked as matures the resighting rate was significantly higher than in those marked as teneral. Similar results were obtained in a population of *S. alpestris* in the Black Forest (Sternberg 1990) as well as in other corduliids such as *Cordulia aenea amurensis* (Ubukata 1975, 1981) and in *C. a. aenea* (Ha 2000).
- (4) Sexual differences in behaviour: The higher resighting rates of males are attributable to their regular presence at the breeding sites and possibly also to their different daily activity. Thus the operational sex ratio of the imagines at the rendezvous in 1998 at (A) was strongly male biased (Knaus 1999). On the average males were resighted 3.8 times after marking, females 1.5 times. Furthermore, the mean interval between successive visits at the breeding site was 3.5 d for males and 9.1 d for females. Males occupied suitable oviposition sites almost continuously. Their activity at the rendezvous lasted 10 h per day and reached its maximum in the late afternoon. Females behaved more inconspicuously and were only sporadically present at the ponds. They arrived in smaller numbers and at a more constant rate over the whole daily activity period (Knaus 1999), possibly also after and before the observers presence (see Sternberg 2000a). On the other hand the mean interval between marking and last resighting was almost equal for both sexes, i.e. 14.6 days and 14.2 days for adult males and females, respectively.

Another variable determining the resighting probability was found by biometrical measurements of *S. alpestris* marked as teneral. Resighted individuals emerged significantly earlier, they had larger exuviae and their wings were longer (Knaus 1999). Thus small, late emerged individuals did not return to the study area after maturation. Three different explanations are possible: (1) high mortality during the maturation period which affects particularly small individuals (see Inden-Lohmar 1997), (2) considerable emigration or immigration from and to surrounding localities (see Pajunen 1966; Soeffing 1990; Inden-Lohmar 1997) or (3) displacement of the late emergers by competi-

tion to suboptimal ponds that were less frequently visited by the observers. Since there was no size difference between resighted individuals that were marked as teneral and those marked as matures, we assume that increased mortality during maturation period is the most likely explanation and only a small part of the population emigrates. This view is supported by the fact that there was no size difference for individuals marked as adults that were resighted afterwards or not (Knaus 1999). Therefore return to the study area after the prereproductive period does not seem to depend on individual body size.

Displacement during and homing after the prereproductive period

For the study area (A), a nearly treeless habitat, it remains unknown where *S. alpestris* spends the prereproductive period. In the Black Forest some marked imagines, between 3 and 8 days old, were resighted in forest within a distance of ca 200 m from the emergence bog waters (Sternberg 1990, 2000a). The obvious scarceness of individuals in the surroundings of emergence ponds at the Bärenseewen plateau indicates that the imagines probably displace considerably during the maturation period. This assumption is supported by the fact that, during the maiden flight, the individuals leave the open terrain of the breeding area and cover long distances (Knaus 2000). They probably spend the maturation period in forested areas further downhill and linger around on the top of the trees where they are hard to detect as assumed in *S. arctica* (Zetterstedt) (Sternberg 2000b). In *C. aenea* immatures were repeatedly seen hunting in forest gaps or clearings in the surroundings of the breeding area, up to 800 m away from the emergence site (Ubukata 1973; Sternberg & Schmidt 2000a; P. Knaus & H. Wildermuth unpubl.). Coincidental observations of other immature corduliids supports the view that the maturation habitat is generally situated in some distance from the breeding site (Valle 1938; Sternberg & Schmidt 2000b).

Individuals of *S. alpestris* marked as teneral were resighted for the first time mainly within the breeding area, but only one male was first seen again at its emergence pond. In contrast, another male was discovered for the first time at a pond 1,700 m away from its emergence site. However, the data available are insufficient for a final statement on dispersal during the prereproductive period; the observation frequency at neighbouring ponds of the Bärenseewen plateau was at this time (i.e. at the end of the prereproductive period) too low. According to various studies it may be assumed that dispersal and emigration takes place mainly during the maturation period, especially when the population density is high as it was in 1998 (Pajunen 1966; Soeffing 1990; Stettmer 1994; Inden-Lohmar 1997; Sternberg 2000a). This assumption is supported by the low resighting rate of imagines marked as teneral and by the significantly higher number of commuting flyers in individuals marked as teneral compared with those marked as adults.

Displacement and site attachment during reproductive period

At locality (A) in 1998 site fidelity was low and the males selected probably only a few ponds for regular and daily visits. This resulted in frequent movements between the ponds. At the Bärenseewen plateau with the water bodies clustered, several suitable ponds on a restricted area were available and the males had the opportunity to

choose and change their rendezvous quickly. Site attachment was limited to the largest ponds. Between successive visits the males probably spent some time in foraging areas, these being 150–1,200 m apart from the Bärenseewen rendezvous on the south-facing slope near the upper limit of the forest where marked males hunted for up to 15 min (Knaus 1999).

18.6% of all marked adults were recorded at least once at ponds outside the marking area of Bärenseewen in distances between 250 and 1,560 m with altitude differences up to 250 m. Presumably, the resighting rate would have been even higher with longer observation periods at ponds outside the marking area. It should also be considered that there were substantial differences between the individual travel distances, hence part of the population was rather resident while another roved about. Altogether, the recorded displacements indicate active exchange between the localities. Some imagines shuttled between the localities. The flights seemed to be well-orientated and even long distances were managed in short time, possibly due to a spatial memory of experienced individuals as also assumed for *S. arctica* and *S. flavomaculata* in corresponding situations (Sternberg 1990; Flöss 1998).

At site (B) in 2000, the results on site attachment and mobility were clearly different from those at (A) in 1998. Although slight exchange between different ponds occurred, site attachment was much more pronounced at (B): 82.9% of all resightings were restricted to the marking locality and only 25% of the adults were observed at least once away from their marking water. At one pond (Anhornen) the resighted males exhibited site fidelity without exception.

Although no marked dragonfly was found to cross the Prättigau Valley we can not exclude the possibility that they did so; our data are too scanty, especially because of the spell of bad weather in July 2000 that affected severely both metapopulations. “Flier”-type Anisoptera are easily able to cover distances of 8 km distant from the marking water as shown in *Aeshna subarctica elisabethae* Djakonov (Sternberg 1995b; for reviews see Corbet 1999 and Sternberg 1999). In this species and in *A. juncea*, Sternberg (1990) also demonstrated an exchange of individuals between two bogs 1.5 km distant from each other. The observed daily flight distance of a few commuting imagines was at least 9 km.

In our study males of *S. alpestris* appeared to be more mobile than females. The same was found in *Plathemis lydia* (Drury) (Koenig & Albano 1987a). However, this may at least be partly an effect of methodological difficulties since females visit the water only shortly for oviposition. In *A. cyanea*, on the other hand, females were found to move farther than males (Inden-Lohmar 1997).

It is striking that residents had significantly longer wings and emerged earlier than commuting fliers (Knaus 1999). Thus it may be assumed that late emergers were driven away from the rendezvous of the larger early emergers. Therefore, the former might have been forced to move longer distances. This corresponds to the fact that resighted individuals had larger body masses compared to non-resighted imagines and that commuting flyers were shorter winged than residents. We may assume that larger males have higher mating success as shown for *A. cyanea* (Inden-Lohmar 1997) and discussed for other Odonata (Sokolovska et al. 2000). Another plausible explanation would be that commuting flyers were harder to detect if they visited only suboptimal or peripheral ponds, i.e. those waters that were less frequently checked by the observers.

Site attachment and displacement at study sites (A) and (B) differed considerably, with site attachment of *S. alpestris* being firmer at (B). Several reasons for the differences may be taken into account:

- (1) Relief, altitude and distances between ponds: Both localities were situated in a comparable, hilly area of the subalpine region on opposite sides of a valley without major differences in relief or exposition. Although site (A) was about 200 m higher than (B) this can be ignored for the question of site attachment and displacement, also because of the nearly identical Odonata fauna at the ponds (P. Knaus & H. Wildermuth unpubl.), resulting in similar competition situations.
- (2) Forest patches as displacement barriers: The exchange of individuals might have been reduced between ponds that were separated by densely forested areas. Especially dark coniferous forest might be avoided by the imagines. On the other hand, orientation in open terrain was perhaps easier (i.e. leaded by linear landscape structures or landmarks), thus promoting regular displacement at site (A). However, we do not know the flight route between the ponds. According to observations by Sternberg (1999) in the Black Forest *S. alpestris* rather flies over treetops than near the ground.
- (3) Weather in different study years: The weather conditions in both study years were different and the cold period in July 2000 affected the survival rate of the imaginal populations at (A) and (B) unequally (Wildermuth & Knaus 2002). Therefore, the results from 1998 obtained at (A) can not be compared unrestrictedly with those from 2000 at (A) and (B).
- (4) Population density: As mentioned above, late emergers were possibly driven away from the rendezvous by the larger, early emergers. This might have been significant in 1998 at the Bärenseewen ponds when population density was high, thus resulting in forced emigration of late emergers as observed in *Leucorrhinia dubia* (Pajunen 1962) and *A. cyanea* (Inden-Lohmar 1997). Therefore, early emerged individuals that were larger, might have resided more commonly near their emergence pond. In *Calopteryx virgo* (Linnaeus), Wildermuth (1986a) reported more intensive dispersal with growing male density, ending up in displacement into suboptimal habitats.
- (5) Mate mating success: Copulation may promote residentiality. Males of *P. lydia* and *A. cyanea* that had mated shortly after arrival at the rendezvous visited the same pond more often than males without mating success (Koenig & Albano 1987b; Inden-Lohmar 1997) and *Libellula depressa* Linnaeus became strongly site attached after successful copulation (Utzeri & dell'Anna 1989).
- (6) Study season: At site (B) our study began slightly later in the season than at (A). It may be supposed that adults were less mobile towards the end of the flying season. However, the data from 1998 at (A) over the complete flying season do not indicate such a bias.

Summing up, it may be said that differences in site attachment and displacement between the localities are mainly due to weather conditions, population density and landscape structure.

Metapopulations and nature conservancy

According to our results the major proportion of the adult *S. alpestris* population disappears from the study area after emergence and only a small proportion returns to the breeding area after maturation. We suppose that the imagines during maturation period show an increased mortality and only a small part of the population emigrates, but it remains unknown where to; the next suitable breeding sites are located 20–30 km distant from our study area. On the other hand we assume that locality (A) and (B) probably harbour two distinct metapopulations (Levins 1970; Hanski & Gilpin 1997). According to Reich & Grimm (1996) all conditions required are fulfilled: (1) The breeding localities are separated thus constituting distinct subpopulations with their own population dynamics, (2) some local populations do not produce imagines every year as shown by quantitative exuviae collection during both study years and may become extinct, (3) there is lively exchange of individuals between the ponds and (4) deserted sites can easily be recolonised. However, the frequency of displacement is apparently different at site (A) and (B), possibly due to structural characteristics of the terrain. But the fractions of residents and wanderers in a metapopulation are probably not only dependent on environmental factors. Obviously each individual exhibits specific behavioural features: some rove about while others seem to be more stationary and site attached, a few even returning to their emergence water. As a consequence from our study, site attachment and displacement in dragonflies should be studied under different environmental conditions, i.e. at various localities over a number of subsequent years, thus giving more insight in the dynamics of metapopulations and its determining factors.

The breeding sites at both of our study areas comprise a number of patchily distributed water bodies differing in structural characteristics such as size, depth and vegetation. Some of them are obviously more suitable for larval development than others. However, for conservation of the metapopulations the entirety of all sites is needed, as Sternberg (1995a, 1995b) pointed out for a comparable situation in *A. s. elisabethae* developing in stem, secondary and latency habitats. In both study areas at least part of the breeding sites are affected by grazing cattle and horses, trampling down the marsh vegetation and eutrophicating the shallow water bodies.

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